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### **A NEW SPECIES OF *HYLA* (ANURA: HYLIDAE) FROM CLOUD FOREST IN OAXACA, MEXICO, WITH COMMENTS ON THE STATUS OF THE *HYLA BISTINCTA* GROUP**

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**ABSTRACT** A new species of *Hyla*, allocated to the *H. bistincta* group, is described from the cloud forest of the Sierra de Juárez and the Sierra Mixe in northern Oaxaca, Mexico. These populations previously were referred to *H. siopela* Duellman, but they differ in features of external morphology, osteology, and larval morphology. The taxonomic status of *H. bogertae* Straughan and Wright is reviewed, and this taxon is placed in the synonymy of *H. crassa* (Brocchi). A revised key and a discussion of the taxonomic status of the *H. bistincta* group are presented.

**Key words:** Anura; Hylidae; *Hyla bistincta* group; *Hyla siopela*; *Hyla celata*; *Hyla bogertae*; *Hyla crassa*; New species; Sierra de Juárez; Sierra Mixe; Oaxaca; Mexico.

**RESUMEN** Se describe una nueva especie del género *Hyla*, del grupo *H. bistincta*, de los bosques nublados de la Sierra de Juárez y la Sierra Mixe, norte de Oaxaca, México. Estas poblaciones se asignaron anteriormente a *H. siopela* Duellman, pero son distintas en ciertas características de la osteología y la morfología de adultos y renacuajos. Se examina el estado taxonómico de *H. bogertae* Straughan and Wright y se ubica a esta especie en la sinonimia de *H. crassa* (Brocchi). Se presenta una clave dicotómica y una discusión sobre el estado taxonómico del grupo *H. bistincta*.

**Palabras claves:** Anura; Hylidae; Grupo *Hyla bistincta*; *Hyla siopela*; *Hyla celata*; *Hyla bogertae*; *Hyla crassa*; nueva especie; Sierra de Juárez; Sierra Mixe; Oaxaca; México.

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Currently, there are 49 recognized species of *Hyla* in Mexico (Liner, 1994; Mendelson and Campbell, 1994; Toal, 1994), 40 of which are endemic to the country. This high number of endemics is likely attributable to the extensive mountain ranges that have produced islands of microhabitats along elevational gradients, a pattern known to exist in birds (Vuilleumier, 1970) and mammals (Brown, 1971). The Sierra de Juárez in central Oaxaca is such an example. A subsidiary mountain chain of the Sierra Madre Oriental, the Sierra de Juárez contains five floral associations along its northern slopes (Bogert, 1968; Wake et al., 1992) that provide a wide variety of microhabitats in which a rich fauna of amphibians and reptiles exists. For example, the type localities for several anurans (e.g., *H. calvicollina*, *H. cyanomma*, *Eleutherodactylus polynniae*), salamanders (e.g., *Thorius smithi*, *Pseudoeurycea saltator*), and squamates (e.g., *Abronia mitchelli*, *Exiliboa placata*, *Cryophis hallbergi*) are found along this slope, and several taxa remain undescribed (Hanken and Wake, 1994). Caldwell (1973) conducted an elevational transect study of the anuran community structure associated with the various habitats along the slopes of the Sierra de Juárez. Part of the material presented herein originated from collections that she made during that study.

Species in the *Hyla bistincta* group (sensu Duellman, 1970) are endemic to the Mexican highlands northwest of the Isthmus of Tehuantepec (Duellman and Campbell, 1992), and range from southwestern Durango east to Puebla and south to the Pacific versant of Oaxaca. These species are of moderate size (>40 mm), and breed in cold mountain streams at elevations from 1400 m (*H. bistincta*) to 3050 m (*H. robertsoni*). Many of these species have restricted distributions; several are known only from the type locality.

Duellman (1968) described *Hyla siopela* from Cofre de Perote in open, dry pine forest of the Sierra de Madre Oriental in central Veracruz from 2500–2550 m. (See Wake et al. [1992] for vegetation types along the north and south slopes of Cofre de Perote.) Caldwell (1974) discovered a population of frogs in cloud forest on Cerro Pelón, the highest peak of the Sierra de Juárez, between 2640 and 2670 m. She referred these specimens to *H. siopela*, thereby documenting an isolated population about 200 km south of the only other known population. Since Caldwell's work, few additional specimens have been collected from this population.

In light of the apparently restricted distributions of many of the species that occur along the slopes of the Sierra de Juárez, we were suspect of the disjunct distribution of the two populations of *Hyla siopela*. Critical examination of the specimens of *H. siopela* from Veracruz and Oaxaca revealed consistent interpopulational differences that led to the investigation of the taxonomic status of the Oaxacan population that we present herein; this investigation supports recognition of this population as a distinct species.

## MATERIAL AND METHODS

Measurements (in millimeters) were made using a Wild M5 dissecting microscope and digital calipers (0.01 mm accuracy) and were rounded to the nearest 0.1 mm; measurements and ratios follow those of Duellman (1970). Terminology follows that of Duellman (1970) and Harris (1979). Characters and measurements used in preparing the taxonomic key were taken from Duellman (1970), and those discovered by direct examination of specimens. Osteological observations were made from radiographs and cleared-and-double-stained specimens (Appendix). Sex was determined by direct observation of the gonads. Museum abbreviations follow standard usage (Leviton et al., 1985). Webbing formulae follow those of Savage and Heyer (1967), as modified by Myers and Duellman (1982). Snout-vent length is abbreviated SVL throughout. A list of specimens examined is given in the Appendix.

## SYSTEMATICS

*Hyla celata* new species

Figures 1–3

**Holotype.**—KU 137103, an adult male, from 0.9 km N Cerro Pelón, Sierra de Juárez, Oaxaca, Mexico, 2670 m (17°30' N, 96°30' W), obtained on 10 June 1970 by Janalee P. Caldwell and Paul B. Robertson. Field number JPC 2474.

**Paratypes.**—KU 137090–92, 137095–97, 137099–100, 137105–10, 137112–14, 137116–18, all males, and KU 137093–4, 137098, 137101–2, 137104, 137115, all females, from 0.9–1.3 km N Cerro Pelón, Sierra de Juárez, Oaxaca, Mexico, 2640–2670 m (17°30' N, 96°30' W), collected between 18 December 1969 and 12 July 1970 by Janalee P. Caldwell and Paul B. Robertson; UTA A-5742 (male), UTA A-5743–44 (females) from 0.7 mi N crest of Cerro Pelón, N slope Sierra de Juárez, Oaxaca, Mexico, collected on 2 April 1978, by J. A. Campbell; UTA A-13380 (female) from 25.4 km S Metates, Sierra de Juárez, Oaxaca, collected on 30 June 1981, by J. A. Campbell.

**Referred specimens.**—See Appendix.

**Diagnosis.**—A moderate-sized, stream-breeding frog distinguished from other Middle American *Hyla* by the following combination of characters: (1) quadratojugal absent; (2) prepollex ossified, enlarged, blunt, bearing small nuptial excrescences in adult males; (3) vertical rostral keel pronounced; (4) skin moderately thick; (5) flanks mottled; (6) vocal slits absent; (7) tarsal fold absent; (8) tympanum and tympanic annulus evident; (9) fingers long with vestigial webbing; and (10) transverse processes on

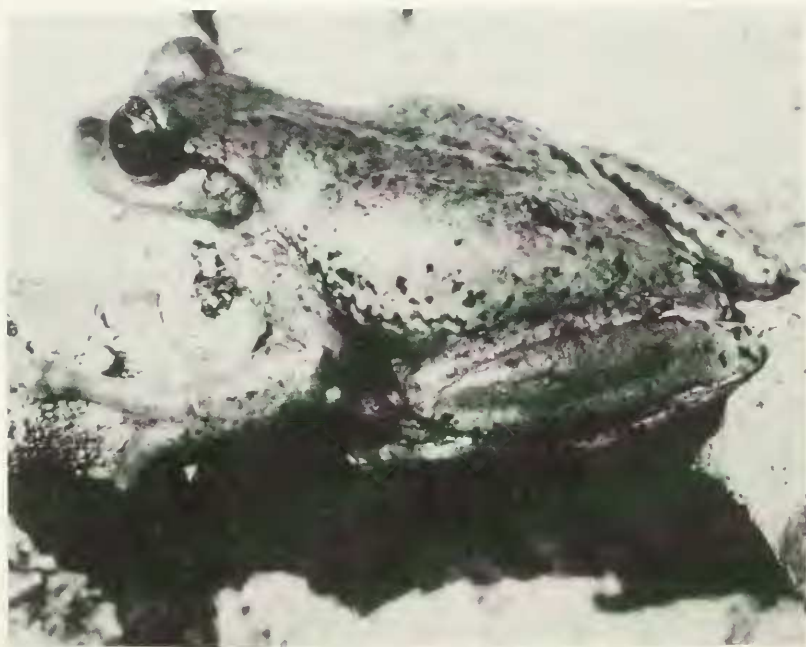


Fig. 1. *Hyla celata* in life. A female (UTA A-13380, paratype), from Cerro Pelón, Oaxaca, Mexico; SVL 36.4 mm. Figure reproduced from UTA color transparency 18153, photographed by W. W. Lamar; specimen collected by J. A. Campbell.

the most posterior presacral vertebra slightly curved, angled  $90^\circ$  with respect to the vertebral column.

*Hyla celata* is most similar to frogs placed in the *H. bistincta* group (sensu Duellman, 1970) in lacking a quadratojugal and having a broad, ossified prepollex. Among these species, *H. celata* is most similar to *H. siopela* (sensu stricto) in coloration and body proportions, but differs by usually lacking a tarsal fold, having a well-defined vertical rostral keel, and slightly curved transverse processes on the most posterior presacral vertebra; the processes are perpendicular to the long axis of the vertebral column. These processes are straight and acutely angled anteriorly in *H. siopela* (Fig. 4). *Hyla celata* can be distinguished from all other members of the *H. bistincta* and *H. arborescendens* groups (sensu Duellman, 1970) by having the following combination of characters: tarsal and thoracic folds absent; tympanum and tympanic annulus evident, distinct; vocal slits absent in adult males; nuptial excrescences present only on prepollex; and rostral keel distinct.

**Description of holotype.**—Adult male; body slender; head as wide as body; head width 31.4% SVL; head length 29.5% SVL. Snout truncate in

profile (Fig. 2), slightly inclined posteroventrally, bluntly rounded in dorsal view with a well-pronounced vertical rostral keel; snout length (anterior margin of eye–anterior margin of head distance) 36.8% head length; rostrum flat; canthus rostralis distinct, rounded; loreal region concave; lips rounded; nostrils ovoid, barely protuberant, directed dorsolaterally, situated  $2/3$  distance from anterior corner of eye to tip of snout; internarial region slightly sloped ventrally. Top of head flat; interorbital distance 31.5% head width; eye diameter greater than eyelid width, 27.8% head width, eyelid width 33.8% head width. Supratympanic fold extending from middle of posterior edge of orbit, adjacent to and obscuring dorsal margin of tympanic annulus, terminating above forelimb at level of ventral margin of tympanic annulus, thick anteriorly, becoming thinner posteriorly; tympanic annulus thin, distinct, protruding above slightly differentiated skin of tympanum; tympanum diameter 54.0% eye diameter; distance between tympanum and eye 1.5 times tympanum diameter.

Axillary membrane absent; thoracic fold absent; fold on wrist slight. Fingers long, bearing slight lateral fringes, terminal discs round. Forearm robust; length of longest finger equal to forearm length; relative length of fingers  $1 < 2 < 4 < 3$ ; disc on first finger as large as tympanum; nuptial excrescences fine, brown, located only on ossified, enlarged, blunt prepollex; subarticular tubercles small, one-third size of thenar tubercle, round, none bifid; supernumerary tubercles numerous, diffuse, present on palmar surface and proximal phalanges of digits; thenar tubercle flat, elliptical, situated upon prepollex midway between proximal phalange of first finger and wrist; palmar tubercle flat, bifid, large lobe three times size

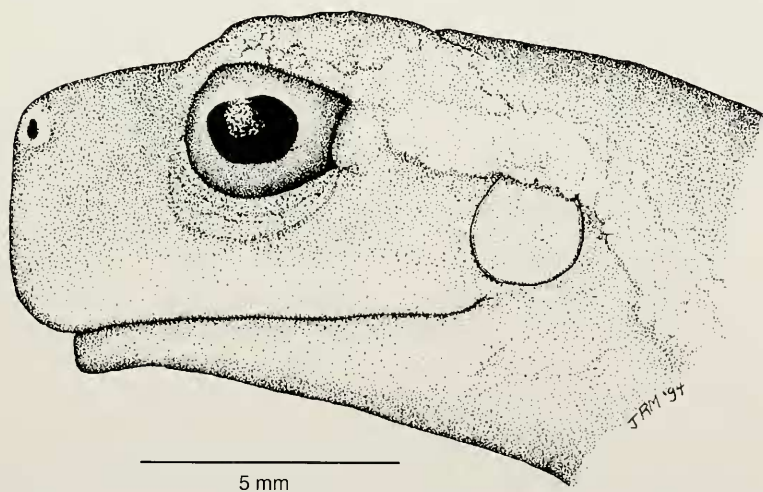


Fig. 2. Profile aspect of head of *Hyla celata* (KU 137103, holotype).



of subarticular tubercles, small lobe equal in size to thenar tubercle; ulnar tubercles and fold absent; webbing on fingers vestigial (Fig. 3). Heels overlapping about one-fourth length of shank when hind limbs adpressed; transverse dermal fold on heel distinct; tarsal fold absent; tibia length 47.6% SVL; foot length 45.9% SVL; inner metatarsal tubercle elongate anteroposteriorly, flat, two times size of subarticular tubercle of first toe; outer metatarsal tubercle absent; length of longest toe equal to length of shank; length of toes  $I < 2 < 5 < 3 = 4$ ; toe discs slightly smaller than those on fingers; subarticular tubercles of toes moderately small, round; supernumerary tubercles numerous, small, flattened, absent from two most distal phalanges of digits; webbing on toes: I  $2\frac{1}{2}$ — $2\frac{1}{2}$  II 2—3 III 2— $3\frac{1}{2}$  IV 3—2 V (Fig. 3).

Cloacal opening directed posteriorly at midlevel of thighs; cloacal sheath short, directed posteriorly; transverse cloacal fold prominent, situated dorsomedially to top of thighs; cloacal tubercles present on ventral surfaces of inner thighs. Skin on dorsum smooth, finely scabrous at midbody (possibly an artifact of preservation); skin on venter finely verrucose; skin smooth on remaining surfaces. Tongue broadly cordiform, free posteriorly, shallowly notched; dentigerous processes situated slightly posterior to level of choanae, transverse, ovoid, bearing five and four teeth, separated medially by a distance equal to distance between ovoid choanae. Vocal slits absent.

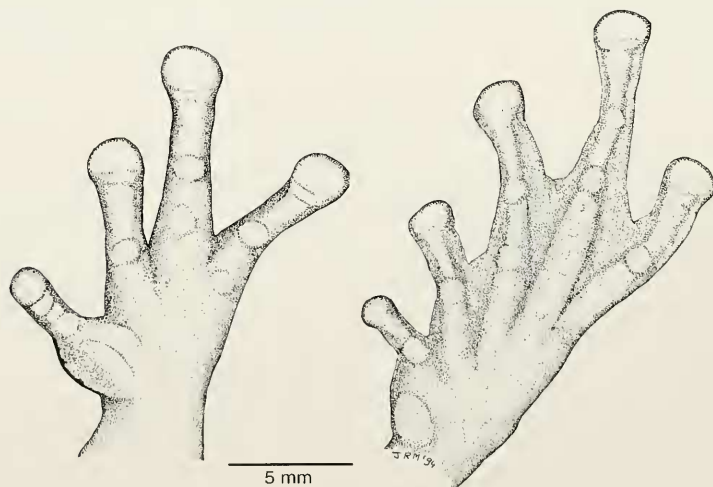


Fig. 3. Ventral aspect of the hand and foot of holotype of *Hyla celata* (KU 137103, holotype). Note the vestigial webbing on the hand. Nuptial excrescences on the ventral surface of the prepollex have been abraded, and are thus not evident from this position.

*Measurements:* Snout-vent length 42.4, forearm length 16.0, tibia length 20.2, foot length (measured from proximal edge of inner metatarsal tubercle to tip of longest toe) 19.5, head length 12.5, head width 13.3, head depth 5.4, snout length 4.6, interorbital distance 4.2, eye diameter 3.7, eyelid width 4.5, tympanum diameter 2.0, internarial distance 4.0.

*Coloration in preservative:* Dorsum and flanks olive-brown with numerous black punctations, reduced on thighs; flanks mottled with white blotches. Venter dull yellow, densely mottled throughout with small brown flecks under 25 $\times$  magnification; posterodorsal surface of cloacal region bearing small white spots; ventral surface of forearm possessing single row of three white spots on left arm, four on right; white spots present around cloacal region; palpebral membrane clear, superior edge densely mottled.

*Coloration in life:* (Fig. 1: UTA color transparency 18153, female paratype UTA A-13380): All dorsal surfaces bronze-brown with scattered distinct black flecks that are most concentrated on the lateral surfaces of the body; canthus rostralis dark brown; dorsal surfaces of fingers dull yellow distally; eye dark brown with thin black reticulations and few, small, red spots near periphery of upper eyelid. The field notes of J. P. Caldwell (10 June 1970) provide the following description: "Dorsum tan with black mottling, covered evenly with bronze chromatophores; abdomen and chin iridescent white; ventral surfaces of limbs pinkish gray; toe pads dull yellow; canthus bronze above, brown below; eyes bronze with black reticulations."

*Variation:* Variation in body measurements between males and females of *Hyla celata* and *H. siopela* are listed in Table 1. Ranges of ratios of those measurements of *H. celata* (males, followed by females in parentheses) are as follows: tibia length/SVL 4.59–5.37 (4.59–5.20); foot length/SVL 4.02–4.67 (4.32–4.70); head length/SVL 2.60–3.27 (2.88–3.12); head width/SVL 2.98–3.23 (2.94–3.27); snout length/head length 3.01–4.33 (2.97–4.70); internarial distance/head width 1.78–2.99 (2.00–2.56); interorbital distance/head width 3.12–3.57 (2.97–3.58); eye diameter/head length 2.58–4.35 (2.76–3.67); tympanum diameter/eye diameter 3.14–6.45 (3.96–6.68).

Information on variation in color-pattern variation among six specimens was taken from the field notes of J. P. Caldwell (11 May 1970; 10 June 1970). No statement of sex was given, but we were able to discern coloration of the holotype by her field notes on 10 June as the "smaller [male] specimen" collected along with a "larger [female] specimen." This provides unequivocal color-in-life data for one male and one female. Color-in-life data for five paratypes are as follow: KU 137102, female, dorsal coloration was leaf-green with brown mottling with bronze chromatophores localized at edges of green on the sides of body and the sides of limbs; KU 137098–101 had dorsal mottling varying from dark green and brown in two individuals to light and dark brown in one individual, and light and dark green in another; sides of the body were delineated from the

Table 1. Comparison of measurements of the type series adults of *Hyla celata* (Pelón) and *H. siopela* (Perote). Mean and standard deviation are given over range in parentheses. TL = tibia length, FT = foot length, HL = head length, HW = head width, ED = eye diameter, EN = eye-naris distance, TD = tympanum diameter, IND = internarial distance, IOD = interorbital distance.

Character	Males		Females	
	<i>H. celata</i>	<i>H. siopela</i>	<i>H. celata</i>	<i>H. siopela</i>
	<i>n</i> = 24	<i>n</i> = 7	<i>n</i> = 15	<i>n</i> = 5
SVL	42.0 ± 1.8 (37.8–56.2)	42.5 ± 3.1 (39.9–44.4)	45.7 ± 4.0 (37.8–51.1)	47.9 ± 2.9 (44.0–51.4)
TL	20.7 ± 0.9 (18.5–21.7)	21.1 ± 0.7 (20.1–22.3)	22.8 ± 1.6 (19.1–24.9)	24.0 ± 0.7 (22.9–24.9)
FT	18.6 ± 0.7 (17.3–19.9)	20.0 ± 0.8 (18.7–21.2)	21.2 ± 1.6 (17.5–24.3)	22.4 ± 0.9 (21.1–23.5)
HL	12.5 ± 0.9 (10.6–13.9)	12.5 ± 0.6 (11.6–13.5)	13.9 ± 1.1 (11.1–15.4)	14.2 ± 0.6 (13.3–15.0)
HW	13.0 ± 0.6 (11.4–14.3)	12.7 ± 0.3 (12.0–13.1)	14.3 ± 0.9 (12.4–15.6)	14.2 ± 1.1 (12.5–15.5)
ED	4.1 ± 0.4 (3.4–4.9)	3.7 ± 0.3 (3.3–4.1)	4.3 ± 0.6 (3.3–5.7)	4.0 ± 0.3 (3.6–4.5)
EN	3.3 ± 0.2 (3.0–4.0)	3.4 ± 0.2 (2.9–3.6)	3.7 ± 0.3 (3.1–4.1)	3.5 ± 0.2 (3.2–3.7)
TD	1.9 ± 0.2 (1.4–2.3)	2.0 ± 0.2 (1.7–2.3)	2.2 ± 0.3 (1.7–2.6)	2.2 ± 0.2 (2.0–2.4)
IND	2.9 ± 0.4 (2.2–4.0)	2.9 ± 0.2 (2.7–3.1)	3.2 ± 0.2 (3.0–3.4)	3.2 ± 0.3 (3.0–3.7)
IOD	4.3 ± 0.2 (3.7–4.6)	4.5 ± 0.1 (4.3–4.6)	4.8 ± 0.4 (4.2–5.4)	4.9 ± 0.3 (4.5–5.4)

dorsum by a variable mottling pattern consisting of dark brown, iridescent copper, light green, and yellow coloration; chin mottling varied from solid brown in some individuals to absent in others; mottling varied from sparse to absent on the abdomen, never covering its entire surface; black dots on the dorsum and flanks of certain individuals are replaced by brown blotches.



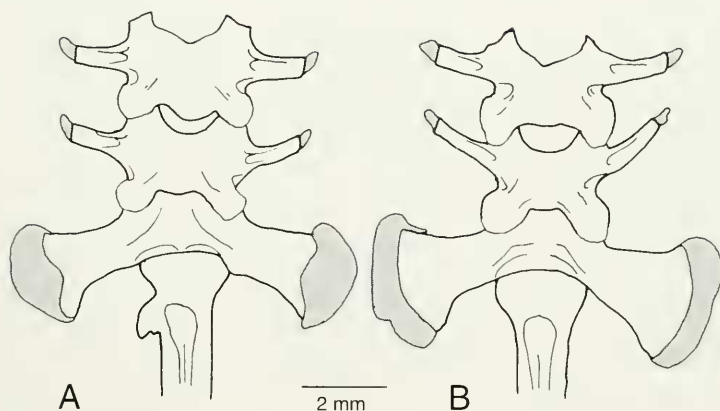


Fig. 4. Dorsal aspect of the presacral vertebrae of *Hyla siopela* (A, KU 137103, holotype) and *Hyla celata* (B, KU 100976, paratype) to show differences in the condition of the most posterior transverse processes. Shaded areas represent cartilage. Note that KU 105629 has an anomalous lateral process on the urostyle.

Ulnar tubercles vary from absent (condition of the holotype) to a series of three to five small bumps on each arm. Males have two to six teeth on each dentigerous process, whereas females have three to six teeth. One adult male (KU 137118) and an adult female (KU 137115) lack dentigerous processes altogether. Nuptial excrescences vary (in preservative) from dull yellow (color of prepollex) to tan or dark brown. In one adult male (KU 137109), the nuptial excrescences have been removed, presumably after preservation.

**Tadpoles.**—Caldwell (1974) provided a complete description and illustration of the tadpole of *Hyla celata* (KU 139841, as *H. siopela*). The tadpoles of *H. celata* are morphologically similar to those of *H. siopela* (described and illustrated by Duellman, 1970), except that those of *H. celata* are larger than those of *H. siopela* at each Gosner stage (Caldwell, 1974). Caldwell (1974) suggested that interspecific competition with sympatric species of stream-breeding frogs at Cerro Pelón, or differences in water temperature between the two localities, might account for the observed differences in overall size of the tadpoles; no other hylids are known to be sympatric with *Hyla siopela*. This hypothesis never has been tested explicitly in these species.

**Distribution and ecology.**—*Hyla celata* is known only from two localities in cloud forest: Cerro Pelón in the Sierra de Juárez and near Santa María Totontepec in the Sierra Mixe. This species is known to breed in mountain streams at elevations of 2640 m and 2670 m on Cerro Pelón. On two separate occasions, specimens were collected from a mossy rock wall

at night sitting in the spray of a small waterfall (field notes of J. P. Caldwell, 1970). J. A. Campbell (pers. comm.) found this species active at 1400 h in direct sunlight on rocks in the middle of a stream, along with individuals of *H. cyanomma*. Bogert (1968) provided a detailed description of the vegetation along the slopes of the Sierra de Juárez.

The cloud forest habitat along the slopes of the Sierra de Juárez has been severely disturbed by logging. J. A. Campbell (pers. comm.) has visited the type locality of *Hyla celata* a number of times since 1980, and has not located individuals of *H. celata*, *H. calvicollina*, or *H. cyanomma*. If these frogs are sensitive to environmental change, as many stream-breeding frogs are, these species may have been extirpated from Cerro Pélón. Additional field work is needed to determine the status of these frogs. There is little, if any, undisturbed cloud forest within ca. 15 km of Santa María Totontepec (field notes of J. R. Mendelson, 17 July 1992). Active searches for hylid frogs were not made during that visit.

**Etymology.**—The specific epithet is derived from the Latin *celo* meaning hidden or concealed, in reference to the way in which specimens of this species were “concealed” under the name *Hyla siopela*.

**Remarks.**—Among some of the referred specimens of *Hyla celata*, we noticed some variation in the diagnostic characters. For example, six individuals (KU 148664–69) from the type locality have more robust bodies, unpatterned venters, and weak tarsal folds. In addition, MVZ 161028 has a tarsal fold and lacks a distinct rostral keel; MVZ 180384 lacks a rostral keel, and CAS 141013 has a distinct tarsal fold. The latter three specimens are from Cerro Pelón. Among the specimens from the Sierra Mixe, UTA A-6843, 6846, and 6936 lack rostral keels. In our experience, some soft anatomical characters, such as tarsal folds, vary among specimens of many species in the *H. bistincta* group and may be affected by different preservation techniques. Nonetheless, we tentatively refer the aforementioned specimens to *H. celata* until more knowledge of variation is obtained from additional material.

In her review of anuran osteological characters, Trueb (1977) suggested that the angles formed by the transverse processes of the vertebrae might be too variable to be informative for elucidating phylogenetic relationships. Although this is the case in her study on *Hyla lanciformis*, we found no intrapopulational variation in the shape, or angle of the leading edge, of the processes on the most posterior presacral vertebra. Thus, we considered the condition exhibited by *H. celata* to be a unique diagnostic character.

Field work by J. A. Campbell and associates from UTA in the Sierra Mixe has resulted in the discovery of populations of *Hyla sabrina*, *H. crassa*, *H. celata*, and *H. arborescendens*. *Hyla sabrina* and *H. celata* otherwise are known only from the Sierra de Juárez, and *H. arborescendens* is known from many localities throughout the Sierra Madre Oriental of

Puebla, Veracruz, and Oaxaca, and in the Sierra de Juárez (Duellman, 1970). Historically, *Hyla crassa* is known from only a few localities in central Oaxaca. (See discussion below.) These findings come as little surprise because a continuous corridor of cloud forest habitat exists through both the Sierra de Juárez and the Sierra Mixe (Campbell and Frost, 1993); several other species of amphibians and reptiles (e.g., *H. chaneque*, *Abronia fuscolabialis*, *Exiliboa placata*) exhibit similar distribution patterns (Campbell and Frost, 1993).

Although the area between the Sierra de Juárez and Cofre de Perote remains poorly known herpetologically, recent field work in the intervening Sierra de Huautla by several parties has not revealed any frogs referable to the *Hyla bistincta* group (Mendelson, pers. observ.; A. Nieto, pers. comm.). This corroborates our hypothesis that *H. siopela* and *H. celata* are indeed allopatric.

## TAXONOMIC NOTES ON THE *HYLA BISTINCTA* GROUP

**The status of *Hyla bogertae*.**—While preparing a key to the species of the *Hyla bistincta* group, we noticed many similarities between the descriptions of *H. crassa* (Brocchi) and *H. bogertae* Straughan and Wright. Duellman (1964; 1970) redescribed *H. crassa* and referred *H. robustofemora* Taylor to the synonymy of this species; at this time only two specimens were available for study. Straughan and Wright (1969) described *H. bogertae* from a series of adults, juveniles, and tadpoles; this species was diagnosed from *H. robustofemora* (= *H. crassa*) based on putative differences in the tarsal fold, foot webbing, and the condition of the prepollex. Caldwell (1974) reported on variation among additional specimens (KU 125354, 139850, 139854, 148696–700) that she referred to *H. crassa* and described the tadpole of this species. All specimens referred to *H. crassa* by Duellman (1970) and Caldwell (1974) are from north of the city of Oaxaca in the Sierra Aloapaneca and the southern slope of the Sierra de Juárez, whereas the type series of *H. bogertae* is from a tributary of the Río Atoyac in the Sierra de Cuatro Venados, about 50 km (by air) SW of the city of Oaxaca. We have examined an additional series of specimens referable to *H. crassa* (UTA A-5786, 5842–43, 5894) that were collected in 1978 in the Sierra Mixe.

Examination of this more recently collected material indicates that the diagnostic characters of *Hyla bogertae* (viz., absence of tarsal fold, less webbing on fourth toe, presence of a single bony element in the prepollex, and absence of webbing on the hand) are present, albeit variable, among specimens referred to *H. crassa*. Among specimens of *H. crassa*, tarsal folds vary from weak (UTA A-5842, male; KU 148696, female) to strong (KU 148697, male; KU 148698, female) and webbing on the fourth toe

may reach the base of the disc (KU 148697, male; KU 125354, female), or not (UTA A-5843, 5894, females). Similarly, the prepollex of *H. crassa* may contain one (UTA A-5842, male) or two (KU 148697, male) elements. Ossification of the prepollex may progress through ontogeny; the larger (presumably older) male specimen that we examined (UTA A-5842, SVL 57.9 mm) has a single prepollical element, whereas the smaller male (KU 148697, SVL 52.9 mm) has two such elements. However, the male allotype of *H. bogertae* is shown by Straughan and Wright (1969) to have a single prepollical element and it is smaller than the specimen of *H. crassa* with which they compared it. Number of elements in the prepollex also may vary without respect to body size (such as in *Pseudacris*, D. Meinhardt, pers. comm.), or may be easily obscured through different radiograph techniques and positioning of specimens (Mendelson, pers. observ.). The amount of webbing on the hand in all specimens examined by us closely matches that of three of the paratypes (KU 152338–39, and LACM 44401 as illustrated by Adler and Dennis [1972:14]). The variation in the degree of concealment of the tympanum by the supratympanic fold noted by Caldwell (1974) is also evident among the UTA specimens from the Sierra Mixe.

Based on this evidence, we hereby place *Hyla bogertae* Straughan and Wright as a junior synonym of *Cauphias crassus* Brocchi 1877. The distribution of this species is now known to include the Sierra Aloapaneca, Sierra de Cuatro Venados, and the Sierra Mixe (sensu Binford, 1989), in the state of Oaxaca, Mexico.

**The status of the *Hyla bistincta* group.**—A number of definitions of the *Hyla bistincta* group have been proposed either explicitly (e.g., Duellman, 1964, 1970; Caldwell, 1974) or implicitly (Duellman and Campbell, 1992). However, none of these is satisfactory under the tenets of the phylogenetic system (Farris, 1979). Each definition promotes the recognition of paraphyletic groups based on combinations of plesiomorphic characters, as is the case with most species groups in *Hyla* (Duellman and Hoogmoed, 1992). In their outgroup analysis of the phylogenetic relationships of *Plectrohyla*, Duellman and Campbell (1992) created a new definition of the *H. bistincta* group; they noted four synapomorphies that united the *H. bistincta* group and *Plectrohyla* as sister taxa. They also identified six synapomorphies that corroborated the monophyly of *Plectrohyla*, but were unable to provide evidence for the monophyly of the *H. bistincta* group (Duellman and Campbell, 1992).

In their reanalysis of the phylogenetic relationships of *Plectrohyla*, Wilson et al. (1994) placed a new species (*P. chrysopleura*) in the genus. Although they recognized the problems of Duellman and Campbell's (1992) outgroup analysis (i.e., the nonmonophyly of the *Hyla bistincta* group), Wilson et al. (1994) did not address these problems. Their cladogram exhibited a greater degree of resolution than that of Duellman and

Campbell, but their result is flawed by the same problems pertaining to outgroup structure and does not clarify the status of the *H. bistincta* group. Given this, the phylogenetic hypothesis proposed by Wilson et al. (1994) for relationships of *Plectrohyla* species should be viewed as preliminary.

As the current taxonomy stands, the *Hyla bistincta* group is defined as those species possessing (1) a long medial ramus of the pterygoid articulating with the otic capsule, (2) thick dorsal skin, (3) continuous fringing papillae on the upper lips of tadpoles, (4) expanded labia with one or more rows of large submarginal papillae medial to the fringing papillae of tadpoles (Duellman, 1970; Duellman and Campbell, 1992), and lacking the synapomorphies of *Plectrohyla*. However, these characters prove to be problematic with regard to their applicability to many species in the *H. bistincta* group. Many species are known from few specimens (e.g., *H. calvicollina*, *celata*, *cembra*, *mykter*, *pachyderma*), thereby rendering osteological comparisons unfeasible. Moreover, larvae of *H. calvicollina*, *cembra*, *charadricola*, *chryses*, *mykter*, *pachyderma*, and *sabrina* are unknown. In addition, the condition of the dorsal skin seems to be defined subjectively among species of the *H. bistincta* group. Compared to other members of this group, *H. charadricola* and *H. chryses* have "thinner skin" (Duellman, 1970:457) and, on this basis, were excluded from the *H. bistincta* group by Duellman and Campbell (1992). Adler and Dennis (1972:15) recognized two "series" of species within the *H. bistincta* group—those with "more glandular skin" (*H. bogertae*, *crassa*, *pachyderma*) and those with "thinner skin" (*H. mykter*, *robertsoni*, *siopela*). Within *Plectrohyla*, dorsal skin is thick and glandular (Duellman and Campbell, 1992). From our examinations, as well as those by the aforementioned workers, dorsal skin thickness is a poorly defined character for these species and varies continuously among them; therefore, we question the utility of this character as providing synapomorphic information for this group of frogs (but see Thiele, 1993).

We agree with Duellman and Campbell (1992) that, in the absence of a phylogenetic analysis, the historical value of the name "*Hyla bistincta* group" should be preserved. However, we think it important to emphasize its typology as being paraphyletic with respect to *Plectrohyla*. As such, we recommend that the definition of Duellman (1970) be followed as a tentative, but more suitable, definition of the *H. bistincta* group. Thus, we place *H. charadricola*, *chryses*, *calvicollina*, *celata*, *cembra*, *cyanomma*, *mykter*, and *sabrina* into the *H. bistincta* group, although perhaps as a "divergence from the main evolutionary line within the [*H. bistincta*] group" (Duellman, 1970:457).

The addition of these frogs to the *Hyla bistincta* group brings the number of species in the group to 14, and others remain undescribed (Toal and Mendelson, pers. obs.; J. A. Campbell, pers. comm). A rigorous cladistic analysis conducted with additional specimens (adults, larvae) of the *H.*



*bistincta* group and *Plectrohyla*, along with additional data sets, hopefully will yield a better understanding of the evolution of this group of Middle American treefrogs. When such an analysis is performed, it should also include *H. arborescendens* and *H. miotympanum*. These two species share many characters with species of the *H. bistincta* group (Duellman, 1970:371–372) and, in fact, may be related closely to these frogs. Only at that time will any hope of delineation of the *H. bistincta* group come to fruition.

## KEY TO THE SPECIES OF THE *HYLA BISTINCTA* GROUP

This key is designed to aid in the identification of live and preserved adults of the *Hyla bistincta* group. We have included *H. arborescendens* in this key because it may be mistaken easily for members of the *H. bistincta* group. (See comments in text.) Many of the characters used in this key are variable; as such, we encourage all users of this key to verify their identifications with the original descriptions or Duellman (1970).

1. Toes webbed to base of disc on all toes (only to middle of penultimate phalange of fourth toe in some specimens); snout distinctly round in dorsal view; heavy supratympanic fold, often concealing tympanum; large size (males to 57.9 mm SVL, females 63.1) ..... *H. crassa*  
 Only fifth toe webbed to base of disc, or not; snout shape and size variable; supratympanic fold weak to moderate, never concealing entire tympanum ..... 2
2. Tympanum and tympanic annulus not evident ..... 3  
 Tympanum and tympanic annulus evident, distinct or indistinct .... 5
3. Nuptial excrescences as enlarged spines; tarsal and thoracic folds present, strong; known only from type locality (Pan de Olla, Sierra Madre Oriental, Veracruz) ..... *H. pachyderma*  
 Nuptial excrescences as fine granules, or absent ..... 4
4. Tarsal and thoracic folds absent; dorsum mottled green, or uniform green; venter tan with dark brown mottling; flanks dark brown, posterior surfaces of thighs dull yellow; eyes red-brown; size small (males to 29.9 mm SVL, females 41.3); known only from the Sierra de Juárez and Sierra Mixe, Oaxaca ..... *H. sabrina*  
 Tarsal and thoracic folds present, weak; dorsum uniform green, sometimes with tiny yellow spots; venter gray, unmarked; flanks and posterior surfaces of thigh pale blue; eyes pale blue; size large (males

- to 56.0 mm SVL, females 64.5); known only from Cerro Pelón, Sierra de Juárez, Oaxaca ..... *H. cyanomma*
5. Vocal slits present; tarsal fold prominent ..... 6  
 Vocal slits absent; tarsal fold weak or absent ..... 7
6. Rostral keel absent; posterior surfaces of thighs with brown reticulate markings; nuptial excrescences covering prepollex and inner surface of second finger in males; size large (males to 53.8 mm SVL, females 67.8) ..... *H. bistrincta*  
 Rostral keel present; posterior surface of thighs without brown reticulate markings; nuptial excrescences covering prepollex only in males; size small (males to 40.0 mm SVL, females 51.6) .....  
 ..... *H. arborescendens*
7. Webbing extending to base of disc on fifth toe ..... 8  
 Webbing extending to middle of penultimate phalange of fifth toe ..... 11
8. Tympanic annulus distinct, at least inferiorly, diameter at least 40% eye diameter ..... 9  
 Tympanic annulus indistinct, diameter less than 40% eye diameter ..... 10
9. Cloacal sheath long; thoracic fold very weak; known from three localities in the Sierra Madre del Sur of Guerrero (Asoleadero, Puerto del Gallo, and Omilteme) ..... *H. mykter*  
 Cloacal sheath short; thoracic fold weak; known from several localities in the pine and pine-fir forests of the Sierra Madre Oriental of Hidalgo and Puebla ..... *H. robertsoni*
10. Nuptial excrescences present; single male 37.0 mm SVL; known only from type locality (33.8 rd km N Candelaria Loxicha, 2160 m, Sierra Madre del Sur, Oaxaca) ..... *H. cembra*  
 Nuptial excrescences absent; size small (males to 44.4 mm SVL, females 50.9); known from several localities in the pine-oak forests of the Sierra Madre Oriental of Hidalgo and Puebla .....  
 ..... *H. charadricola*
11. Lateral surfaces of head, body, and limbs darker than dorsum, with distinct dark brown markings; size large (males to 52.1 mm SVL, females 56.4) ..... *H. pentheter*

- Lateral surfaces of head, body, and limbs paler than dorsum, without distinct dark markings ..... 12
12. Distinct thoracic fold and tarsal fold present; rostral keel absent; size small (males to 41.1 mm SVL, females 44.0) ..... *H. chryses*  
 Thoracic fold absent; tarsal fold and rostral keel present or absent; size variable ..... 13
13. Tarsal fold absent; dorsum of rostrum concave in profile; rostral keel present; tympanum indistinct; fingers short, with broad lateral fringe; known only from Cerro Pelón, Sierra de Juárez, Oaxaca .....  
 ..... *H. calvicollina*  
 Tarsal fold and rostral keel present or absent; rostrum flat in profile; tympanum distinct; fingers long, without broad lateral fringe ..... 14
14. Rostral keel weak or absent; tarsal fold weak; known only from Cofre de Perote, Veracruz ..... *H. siopela*  
 Rostral keel strong; tarsal fold absent; known only from the Sierra de Juárez and Sierra Mixe, Oaxaca ..... *H. celata*

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## APPENDIX

Specimens examined and their localities. All specimens are post-metamorphic and preserved in fluid, unless otherwise noted. Holotype and paratypes of *Hyla celata* are not included herein.

### *Hyla arborescandens*

MEXICO: *Oaxaca*: Sierra Mixes, 13.6 mi [21.9 km] (by road) NE Tamazulapan, UTA A-5761–62, 5891–92; Sierra Mixes, 3.6 mi [5.8 km] (by road) W Totontepec, UTA A-5763–67, 5774–75, 5777–81; Sierra Mixes, 11.4 mi [18.4 km] W (by road) W Totontepec, UTA A-5801–06; Sierra Mixes, Totontepec, UTA A-5838–39; Sierra Mixe, 3.1 mi [5.0 km] W Totontepec, UTA A-6846, 6933; Sierra Mixe, 5.6 km W Totontepec, 2121 m, UTA A-13196.

### *Hyla calvicollina*<sup>2</sup>

MEXICO: *Oaxaca*: Sierra Juárez, 4 km N Cerro Pelón, 2518 m, KU 186356 (holotype); Sierra de Juárez, 0.7 mi [1.1 km] N Cerro Pelón, 2712 m, UTA A-5059 (paratype).

### *Hyla celata*

MEXICO: *Oaxaca*: Sierra Mixes, 3.1 mi [5.0 km] W Totontepec, UTA A-6936, 6843–46; bus stop shed, Cerro Pelón, 15.0 km SW Vista Hermosa on MX Hwy. 175, MVZ 180384; 52–54 km (by road) N of Guelatao, N slope Cerro Pelón on MX Hwy. 175, MVZ 161028; Distrito Sola de Vega, 2 km below Cerro Pelón, CAS 141013; 0.9 km N Cerro Pelón, 2670 m, KU 137089 (cleared-and-stained).

<sup>2</sup>Toal (1994) described *Hyla calvicollina* from the Sierra de Juárez, Oaxaca.



*Hyla cembra*

MEXICO: *Oaxaca*: Campamento Río Molino, 2160 m, KU 137035 (holotype).

*Hyla charadricola*

MEXICO: *Puebla*: 14.4 km W Huachinango, 2280 m, KU 58414 (holotype). 53813–15, 152367–68.

*Hyla chryses*

MEXICO: *Guerrero*: between Puerto Chico and Asoleadero, 2540–2600 m, UMMZ 125374 (holotype), KU 106306 (paratype); Sierra Madre del Sur, 0.6 km SW Carrizal de Bravos, 2200 m, AS 142452–53; Sierra Madre del Sur, 5.5 km SW Carrizal de Bravos, 2523 m, CAS 142938–50; Sierra Madre del Sur, Carrizal de Bravos, 2505 m, CAS 143926–29; 4 km WNW Carrizal de Bravos, 2579 m, MVZ 112330–32.

*Hyla crassa*

MEXICO: *Oaxaca*: 9 mi [14.5 km] NE Oaxaca, KU 125354; 1.9 km S El Estudiante, ca. 1850 m, KU 148696–700; tributary of Río Atoyac below Vivero El Tapanal, 1.6 km S La Cofradia, 2652 m, KU 152338–40 (paratypes of *H. bogertae*; 152340 = tadpoles); 6.3 km SE Ixtlán, 1910 m, KU 139850 (tadpole); 2.3 km E and 11.6 km NE Oaxaca, 1720 m, KU 139854 (tadpoles); Sierra Mixes, 3.6 mi [5.8 km] W (by road) Totontepec, UTA A-5786, 5842–43, 5894; Cerro San Felipe, UIMNH 25050 (holotype of *H. robustofemora*).

*Hyla cyanomma*

MEXICO: *Oaxaca*: 31.2 mi [50.2 km] N Guelatao, 9600 ft, KU 100507; 1.2 km N Cerro Pelón, 2650 m, KU 148656–63, 152370–72; Cerro Humo Chico (= adjacent to Cerro Pelón), UIMNH 73892–98.

*Hyla mykter*

MEXICO: *Guerrero*: 11.4 km (by road) SW of Puerto del Gallo, 1985 m, KU 137553 (holotype); Asoleadero, 2520 m, KU 137552 (paratype); 1.6 km N Puerto del Gallo, 2438 m, UTA A-4108, 4110–11; 0.8 km SW Omilteme, UTA A-4904; 12.4 km SW Filo de Caballo, near intersection with Chichihualco road, UTA A-13364.

*Hyla pachyderma*

MEXICO: *Veracruz*: Pan de Olla, S of Tezuitlan (Puebla), USNM 115026–27 (paratypes).

*Hyla pentheter*

MEXICO: *Oaxaca*: 32.9 km N San Gabriel Mixtepec, 1530 m, KU 136886–88.

*Hyla robertsonum*

MEXICO: *Hidalgo*: El Chico Parque Nacional, 3050 m, KU 71265–95.

*Hyla sabrina*

MEXICO: *Oaxaca*: 11.1 km S Vista Hermosa, 1840 m, KU 137044 (paratype); 11.6 km S Vista Hermosa, 1910 m, KU 137053 (paratype); 11.9 km S Vista Hermosa, 1920 m, KU 137059–60, 137064, 137066, 137069–72 (paratypes); 12.3 km S Vista Hermosa, 1920 m, KU 137076 (paratype); 15.8 km S Vista Hermosa, 1990 m, KU 137085 (paratype); 16.6 km S Vista Hermosa, 2020 m KU 137087 (paratype); 25 mi [40.3 km] S of Valle Nacional, UTA A-4357; Sierra Mixes, 3.6 mi [5.8 km] (by road) Totontepec, UTA A-5771, 5776, 5782–83; Sierra Mixes, Totontepec, UTA A-5838.

*Hyla siopela*

MEXICO: *Veracruz*: W slope Cofre de Perote, 2500–2550 m, KU 100976–80 (paratypes), 100981 (holotype), 100982–85 (paratypes), 100986–94, 105628 (paratype) 105629 (cleared-and-stained, paratype), 105630–34; Rancho El Capulio, 7 km SE Perote, 2920 m, KU 129163.